A REVIEW OF SALINITY REQUIREMENTS FOR SELECTED INVERTEBRATES AND FISHES OF U.S. GULF OF MEXICO ESTUARIES

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ABSTRACT

Salinity has a pervasive influence on the natural history of estuarine organisms, affecting every major aspect of their lives. Despite the importance of salinity in the study of estuarine ecology, little is known of its effects on the different life stages of estuarine organisms. Changes in estuarine salinity regimes due to anthropogenic modifications further complicate efforts to understand how salinity affects these animals. Literature concerning the salinity requirements of 56 selected estuarine species and the effects salinity has on these species were surveyed for this report to help fill the void of information on salinity requirements as well as identify fish and invertebrate species and their life stages most susceptible to salinity variability. Species were chosen on the basis of their commercial, recreational, or ecological importance or their value as indicators of environmental stress. Many species meeting the criteria for inclusion in the summary table were omitted due to lack of data. Some eligible species were included even though little data about them were available to illustrate the lack of salinity information on many important estuarine species. An overview of salinity tolerance and preference ranges for each life stage of selected species along with pertinent references were compiled and tabulated. In addition, the effects of salinity on general aspects of estuarine organisms (distribution, temperature response, reproduction, physiology, growth, food and feeding, and behavior) are summarized and discussed. The discussion is illustrated with specific examples of salinity effects on some of the selected species. Several conclusions were drawn concerning how salinity and estuarine organisms interact. Fluctuations in salinity are an integral part of the estuarine environment, and estuarine organisms have evolved a characteristic set of mechanisms for responding to these variations. These mechanisms are influenced by

acclimation, adaptation, stage of development, environmental conditions, and the rate and magnitude of salinity change. Different populations of a species appear to have adapted to the specific salinity regime of their area and their tolerance to salinity may differ from that of other populations. The salinity tolerance of all life stages of different estuarine species is not well known, but egg and larval stages appear the most vulnerable to salinity fluctuation. Estuarine animals exist together in a community assemblage; thus, the influence of salinity on one species can be extended either directly or indirectly to affect other species. Species with sparse to no data were generally those without economic value, although many are ecologically important. Salinity dictates the distribution of life in estuaries because of its intimate interaction with both individual and groups of species, underscoring the importance of gaining a thorough understanding about its nature and the way it affects estuarine ecology.

INTRODUCTION

In estuaries, physical factors play a significant role in determining population dynamics (Kinne 1967). Salinity has traditionally been a central parameter for estuarine analysis, particularly as an indicator of estuarine hydrography and habitat potential (Ward and Armstrong 1980, Orlando et al. 1993). Because salinity directly affects the distribution, abundance and composition of estuarine flora and fauna, it is an essential element in determining estuarine habitat (Reid 1961, Chapman 1966, Green 1968, Deegan et al. 1986, Bulger et al. 1990, Orlando et al. 1993).

The estuary is a dynamic environment where freshwater and seawater are mixed. One of the chief characteristics of this environment is that at any location, salinity fluctuates over time and in some places may be highly variable. Estuarine salinities can range between freshwater (<0.5‰) near the source of freshwater input to full seawater (30-40‰) in the lower estuary near ocean passes and inlets. As a result, estuarine fauna can consist of species from both freshwater and marine environments, species migrating from one environment to the other, and a small number of resident species (Green 1968, Perez 1969, Zottoli 1973, Vernberg and Vernberg 1981, Moyle and Cech 1982). The mixing of fresh and salt water and rapidly changing salinity levels in estuaries create harsh physical and chemical conditions with which estuarine organisms must cope. Estuarine animals expend considerable amounts of energy adjusting to changing conditions or by moving about in search of less stressful conditions. However, the same factors that create these harsh conditions also concentrate nutrients at levels that can support large populations of food organisms, making the estuary one of nature's most productive systems. Estuarine productivity provides an enormous energy source to its inhabitants which more than compensates for the rigors of their environment. Estuaries have long been recognized as important nursery areas for young fishes and invertebrates because they provide primary habitat for pre-adult life stages, rich food resources, and protection from predators (Haedrich 1983, Czapla et al. 1991). Many of the species that use estuarine nursery areas (estuarine-dependent species) are taken by recreational and commercial fishermen and support important fisheries.

Although a preponderance of animals in the estuary are juveniles, few consistent and comprehensive data bases exist which allow examination of the relationships between distribution of early life stages and salinity patterns in estuaries (Czapla et al. 1991). Much of the distribution and abundance information for estuarine-dependent species is for offshore life stages and does not adequately describe estuarine distributions, or is for a relatively few important commercial and recreational species. Information on salinity tolerances in particular is incomplete and difficult to find because it occurs as side issues in articles dealing with other subjects (Gunter 1956, Haedrich 1983, Peterson and Meador 1994). In addition, the natural salinity range of a species is frequently narrower than its experimentally demonstrable tolerance (Gainey and Greenberg 1977). Consequently, the effects of salinity on the different life stages of many fish and invertebrate species are not well known.

Estuarine salinity is subject to wide temporal fluctuations that may occur annually, seasonally, or tidally. Salinity can also vary spatially within an estuary, especially with changes in depth (de Sylva 1975). In addition to natural forces of variation, most estuaries of the United States (and their watersheds) have undergone significant anthropogenic modifications which changed their salinity structure (Chapman 1966, White and Perret 1973, Orlando et al. 1993). The more drastic changes include: stabilization of major tidal inlets and construction of navigation channels which promote saltwater intrusion, flow diversions and reservoir construction which may alter the volume or timing of freshwater discharge to the estuary, and large-scale disposal of dredge material (including construction of diked disposal islands) which modify circulation patterns. As a result, salinities throughout an estuary may undergo important historical alterations completely unrelated to the estuary's natural variability.

The cumulative effects of even small changes in many estuaries may have a total systemic effect throughout large portions of the Nation's living estuarine and marine resources and those economic activities that depend on them (Monaco and Emmett 1988, Bulger et al. 1990, Orlando et al. 1993). Therefore, the development of life history information on salinity tolerances of estuarine species is necessary for understanding the impact of changes in estuarine salinity patterns on animals and for implementing management strategies to cope with these changes.

The objective of this paper is to characterize the salinity tolerance of selected estuarine invertebrates and fishes throughout their life history in order to identify those species and life stages most susceptible to salinity variation. We reviewed existing literature to determine the scope and content of salinity information available for each eligible species and to ascertain how these species are affected by salinity.

This report is intended to improve understanding of the relationship between estuarine salinity patterns and estuarine productivity. Data provided in this report should improve the ability of resource managers to anticipate the effects of salinity-pattern modifications on the biology of estuarine organisms. In addition, our review of the literature on this topic documents areas where data are lacking and those issues that require more research.

DATA COLLECTION AND ORGANIZATION

Fifty-six estuarine species were selected, and existing information concerning the salinity requirements for these species throughout their development was reviewed, evaluated, and summarized. Species were chosen for inclusion in our survey if data on salinity tolerance existed for the species and at least one of the four following criteria was met (Czapla et al. 1991):

1) Commercial importance - species in inland or marine waters that fishermen harvest for the purpose of deriving income by their sale. Commercial species were determined by review of catch data and value statistics from the National Marine Fisheries Service (NMFS) and state agencies.

2) Recreational value - species targeted by recreational fishermen that may or may not be of commercial importance. These species were determined by consulting regional experts and NMFS reports.

3) Indicator species of environmental stress - species that either have a strong association with bottom sediments through a benthic life style or consume benthic organisms. Monitoring physiological disorders in this group can indicate episodes of environmental pollution and/or stress. These species were identified from the literature, discussions with fisheries experts, and from monitoring programs such as NOAA's National Status and Trends Program.

4) Ecological value - species that are important because of one or more of the following attributes: specific trophic level occupied; relative abundance; and evidence of importance as a key predator or prey species.

After species were selected, a life history table outlining all life cycle stages was constructed to show how salinity affects those organisms throughout their lives. Information for the table was gathered from scientific journals, unpublished reports, and graduate studies. Topics covered the life histories of species throughout the Gulf of Mexico and represent data collected over several years. In addition, regional and local experts were consulted to complement data from the literature. These consultations were especially helpful in providing estuary/species-specific information, additional references and contacts, as well as suggestions about what species to include in the study. Several texts and journals articles dealing with physiological mechanisms were also used to summarize the principal ways salinity affects estuarine organisms and the means these animals use to cope with salinity change. This was done to show the importance of salinity and to provide a greater understanding of the information presented in Table 1.

RESULTS AND DISCUSSION

A total of 14 invertebrates and 42 fishes were selected for study, and salinity requirements for spawning, egg, larva, juvenile, and adult life stages of each species are summarized in Table 1. Many other species met our criteria for inclusion in the study, but were omitted because little data exist (e.g., bay whiff *Citharichthys spilopterus*, bighead searobin *Prionotus tribulus*, inshore lizardfish *Synodus foetens*, least puffer *Sphoeroides parvus*). The bay whiff, for example, is one of the most common small flatfish in the Gulf of Mexico (Hoese and Moore 1976), and although this species is probably an important predator on benthic fauna, very little is known about its different life stages (Martin and Drewry 1978). Other species were included in our study, even though salinity data were limited, to illustrate where gaps in these data exist (e.g., lesser blue crab *Callinectes similus*, scaled sardine *Harengula jaguana*, bayou killifish *Fundulus pulvereus*, saltmarsh topminnow *Fundulus jenkinsi*). Most of these species with little or no data are small, secretive, and occur in low densities. Although they may be ecologically important, they have little to no economic value. The majority of organisms listed in Table 1 are well known commercial and recreational species illustrating that the research effort expended on estuarine species is directly related to their economic importance.

The animals we selected based on the criteria above are either estuarine residents (organisms that live in the estuary throughout their lives) or migrants (marine species that utilize the estuary during some portion of their life cycle). Both resident and migrant species must withstand wide ranges of salinity and strong salinity fluctuations (tides, floods, etc.) common in estuaries. Residents are typically euryhaline throughout their life cycle, whereas migrants appear to have their greatest tolerance only during that period (usually pre-adult stages) when they occur in the estuary (Table 1). Migrants typically spawn at sea and their young are transported into estuaries by various mechanisms where they grow and develop toward adulthood. As they grow, the young move into the lower parts of the estuary and finally back into the open sea. Migrant species are typically large, strongly motile organisms, whereas residents are generally sessile or small, and weakly motile.

Because of these differences in life style, the manner in which the two groups respond to changes in salinity can be very different. Motile organisms can move very quickly to more tolerable regions, whereas weakly motile or sessile animals either relocate more slowly by passive means or eventually die. Reproduction can also be affected. Motile animals can seek a more suitable area for reproduction, whereas relatively non-motile organisms must delay reproduction or may be forced to spawn in conditions that are either lethal to eggs and larvae or result in poor growth conditions for their offspring.

Both habitat requirements of species and habitat conditions brought about by salinity changes vary temporally in estuaries. To survive and thrive, a species' salinity requirements must match estuarine conditions during its time of residence in the estuary. That is, each species not only requires certain salinities, but it needs these salinities during specific times of the year (when it occupies estuarine habitats). Nelson et al. (1992) present information on times of estuarine residence by life stage for 44 species common in Gulf of Mexico estuaries.

Salinity events which affect the recruitment or habitat suitability of an organism can also result in distributional changes affecting predator-prey relationships. Estuarine species exist together in community assemblages, and alterations of the density patterns of predator or forage species can lead to still further changes in the distribution of other organisms associated with them.

Although most of the organisms listed in Table 1 tolerate a wide range of salinities, ranges and preferences were generally much broader when considered collectively throughout their range across the Gulf of Mexico and over long-term periods than they were in local areas and on a short-term basis. Several factors may account for the apparent ability of species to tolerate a wide range of salinities including: behavior, physiological mechanisms, environmental parameters, acclimation, and adaptation.

Behavioral/physiological adaptations

The responses to salinity that occur throughout the life history of estuarine animals are not open to simple explanations. The effects salinity has on these animals are often the net result of a number of factors in addition to the salt content of the water (Holliday 1971, Longley 1994). Environmental variables such as oxygen content, water density, and the ionic composition of water can all influence how an animal reacts to salinity. Salinity can affect organismic functions and structures differently at different ontogenetic or physiological stages. In addition, events occurring at any one time in the life of an animal can be determined, at least to some extent, by the conditions experienced at some earlier stage of growth and development.

To thrive in an estuary, organisms must be able to withstand extreme ranges and fluctuations of environmental factors such as salinity. Estuarine organisms possess a number of physiological mechanisms which allow them to tolerate rapid changes in salinity (Kinne 1967). These mechanisms can be grouped into four broad categories: escape, reduction of contact, regulation, and acclimation.

Escape.

Escape to salinities that are more suitable is limited to mobile organisms and to situations in which suitable conditions are both available and accessible (Kinne 1967). Both horizontal and vertical migrations may be used to avoid unfavorable salinities. For example, exceedingly abrupt declines in salinity can cause mass movements of spotted seatrout *Cynoscion nebulosus* to more saline areas of the estuary, whereas juveniles of this species tend to avoid hypersaline conditions (Simmons 1957, Tabb 1966). Juvenile Atlantic croaker *Micropogonias undulatus* tend to avoid areas of fluctuating salinity and are usually most abundant in areas of relatively stable salinity (Diaz and Onuf 1985). Laboratory studies suggest that Atlantic croaker, as well as spot *Leiostomus xanthurus*, generally avoid areas of sudden salinity change (Perez 1969). Changes in salinity also affect the movements of juvenile penaeid shrimp *Penaeus* spp. and red drum *Sciaenops ocellatus* in the estuary (Simmons 1957, Gunter 1961, Minello et al. 1990). Adults that spawn offshore (e.g. gulf menhaden, red drum) may take advantage of estuarine salinities by using salinity gradients present in estuarine and oceanic areas as orientation cues for directed migrations to and from spawning grounds (Holcomb 1970, Odum 1970, Owens et al. 1982). Such an orientation system would be particularly useful for species in moving between estuaries and the Gulf of Mexico.

Salinities are usually more stable in or near the substrate than in the upper water column, and average salinity may differ between surface and bottom waters (Kinne 1967). This is particularly true in the tidal mixing zone where the relative proportions of seawater and freshwater change regularly. Therefore, animals can migrate vertically to escape unfavorable conditions by taking refuge in deeper, more stable waters during periods when salinities in the upper water levels become stressful. The preference Atlantic croaker appears to have for deep tidal creeks in some strongly tidal estuaries may be due at least in part to avoidance of rapidly fluctuating salinities in shallow flats and marsh creeks (Diaz and Onuf 1985). The Atlantic brief squid *Lolliguncula brevis* thrives in high-salinity bottom waters, although it may briefly venture into overlying low-salinity surface waters to forage (Hendrix et al. 1981). Some animals (e.g. the lightning whelk and the moon snail Pomatoschistus microps) can escape stressful salinities by burrowing into bottom sediments (Hendrix et al. 1981).

Animals can also take advantage of various environmental factors, such as temperature, that may counteract, support, or modify the physiological effects of salinity (Kinne 1967). When salinities reach extreme levels and areas with more favorable salinities are not readily available, regions with suitable temperatures can be utilized as refuges until conditions improve. In the Laguna Madre of Texas, many species normally intolerant of hypersaline conditions common to the area, such as the blue crab *Callinectes sapidus*, red drum, and flounders *Paralichthys* spp., were present during high salinities periods that coincided with low temperatures (Simmons 1957).

Reduction of Contact.

Reducing contact with the medium is a temporary measure made in response to adverse salinity conditions (Kinne 1967). Different responses that fit this strategy include: production of slime, mucus, or other protective substances that cover the body surface; retreat into burrows or holes, which may sometimes be plugged; reduction of surface to volume ratios of organs or the whole body through muscular contractions; withdrawal of sensitive body parts; closure of shells or comparable structures; and actual changes in body form and other structural properties during periods of prolonged salinity stress. This strategy is employed by the American oyster *Crassostrea virginica* and hard clams *Mercenaria* spp. When salinity reaches stressful levels, both species will close their shells tightly and respire anaerobically until salinity returns to more suitable levels (Galtsoff 1964, Eversole 1987).

Regulation.

Animals can also use internal regulatory devices such as ion regulation, volume regulation, and osmoregulation to maintain themselves when salinities reach stressful levels (Kinne 1967). Ion regulation is one of the most universal functions of living things (Prosser 1973). Generally, an animal's body fluid and tissues maintain potassium and hydrogen ions above, and sodium and chloride levels below that of undiluted seawater, while excluding magnesium and sulfate (Kinne 1967). Ion regulation occurs both between the external medium and blood as well as between blood and tissues. High capacities for ion regulation, tissue tolerance to fluctuations in ionic ratios, and possible osmotic stabilization by means of dissolved organic substances are important physiological prerequisites for successful estuarine establishment. Most molluscs (e.g. common rangia *Rangia cuneata*), decapod crustaceans (e.g. blue crab, penaeid shrimp), teleosts, and elasmobranchs use ionic regulation to maintain the osmotic pressure of their blood when that of the surrounding medium drops below ideal levels (Robertson 1957, Kinne 1967, Prosser 1973, Deaton 1981, Moyle and Cech 1982).

Volume regulation appears to be an important ability of most estuarine species (Kinne 1967). When a sudden change in salinity occurs, volume regulators not only lose or gain water, but also lose or gain salts. A change in volume is indicative of a distortion in the steady state balance of the continuous inflow and outflow of water and salt. Such distortion initiates a whole series of responses and adjustments leading to changes in permeability and excretory processes, and finally to a new steady state balance between the organism and its external medium. In molluscs, which use an intracellular pool of amino acids to regulate cell volume, differences in salinity tolerance have been linked to differences in the capacity of this pool (Gainey and Greenberg 1977).

Acclimation.

The majority of estuarine organisms have the capacity for osmoregulation (Kinne 1967). The proper balance of water and electrolyte levels often involves several organs or organ systems, and may be under the control of the endocrine and nervous systems. The main osmoregulatory organs are gills which are often responsible for salt balance, the gut which is often responsible for water balance, antennal glands (some crustaceans), and body surfaces. Estuarine animals are also able to acclimate to changing levels of salinity. This is a process in which physiological adjustments to a new environment varying in one or two parameters (e.g. salinity, temperature, etc.) act to increase an animal's capacity to survive, reproduce, or compete (Kinne 1967, Hill 1976, Lankford and Targett 1994). Animals are thus able to compensate for adverse environmental conditions and regain physiological stability and internal homeostasis. The abilities to both tolerate and acclimate to salinity in early animal life stages may be influenced by factors such as stage of development, nutritional status, season of larval release, single or multiple environmental factors, amplitude and rate of change of environmental fluctuations, acclimation, and geographical origin of the populations (Sastry 1983).

Physiological regulatory responses to salinity can be very rapid (Holliday 1971). This is important because organisms in estuaries are affected by the rate as well as the magnitude of salinity change (Simmons 1957, Green 1968, Darcy 1983, Zimmerman et al. 1990). Reid (1954) reported large numbers of pigfish *Orthopristis chrysoptera*, pinfish *Lagodon rhomboides*, silver perch *Bairdiella chrysoura*, gulf killifish *Fundulus grandis*, pipefishes *Sygnathus* spp., inland silverside *Menidia beryllina*, crevalle jack *Caranx hippos*, and other species were killed when a hurricane struck Florida and lowered salinity from 23.5 to 9.7‰ over a four day period. The rapid drop in salinity, rather than the low salinity itself, is thought to have caused the fish kill (Darcy 1983). The speed of salinity change rather than the magnitude was found to induce short-term stress responses in juvenile spot (Moser and Miller 1994). In order to withstand rapid fluctuations, the ability of estuarine animals to tolerate fast changes in the external environment must be linked with the ability to regulate their internal environment. Thus, rate of acclimation to salinity change is important if an animal is to become a permanent and successful estuarine dweller (Green 1968, Moser and Miller 1994). For example, the white shrimp *Penaeus setiferus*, which can tolerate sudden salinity drops more readily than the brown shrimp *Penaeus aztecus* (Minello et al. 1990, Longley 1994), is more able to exploit the lower salinity zones of an estuary.

In many cases, physiological capacities for living in extreme environments are gained or lost during the life cycle (Kinne 1967). In order to survive and grow in an estuary, an animal must be able to accommodate to this environment at all stages of its life cycle that are present in this habitat. The salinity tolerance of many organisms becomes greater as they develop toward adulthood as the data in Table 1 illustrate. The eggs and larvae of many euryhaline fish and invertebrates (e.g., common rangia, pink shrimp *Penaeus duorarum*, white shrimp, crevalle jack, gizzard shad *Dorosoma cepedianum*, snook *Centropomus undecimalis*, spadefish *Chaetodipterus faber*) survive well only in salinity ranges that are much narrower than those of adults. These early stages do not possess the differentiated organs and tissues employed by adults in osmotic-ionic regulation and must initially depend on chloride cells in their epithelium to perform this function. In order for the gill, gut, and renal structures to become functional, they must undergo gradual anatomical and physiological development and thus may not become fully functional until an animal has reached a certain point in its development. In addition, young stages have high surface-to-volume ratios, and although eggs, cleavage stages, and larvae may be encased in relatively impermeable membranes, newly hatched young are frequently characterized by thin and delicate integuments. These factors can aggravate problems with passive water and solute exchange. There are several examples of this phenomenon. Eggs and larvae of gulf menhaden *Brevoortia patronus* and striped mullet *Mugil cephalus* are stenohaline and associated with high-salinity Gulf waters, whereas later stages are considered euryhaline (Christmas et al. 1982, Nordlie et al. 1982). Pre-juvenile Atlantic brief squid do not appear to be as euryhaline as adult squid, and in coastal Louisiana waters, are not found in salinities below 22‰ (Vecchione 1991). Atlantic croaker and spot also seem to become increasingly tolerant of higher salinities as they grow larger (Diaz and Onuf 1985, Moser and Miler 1994).

For some species, however, the regulatory abilities of the young are greater than those of adults (Holliday 1971, Hill 1976). It may be that in these cases the relatively undifferentiated cells of the embryo and early larva are more tolerant than the highly specialized tissues of later life stages (Holliday 1971). Size in penaeid shrimp (postlarval and larger) is positively correlated with salinity tolerance (Williams 1955, Zein-Eldin and Griffith 1969). Small shrimp are found in the less saline portions of nursery areas, whereas progressively larger shrimp occupy higher salinity regions nearer the sea. Spotted seatrout, which usually complete their entire life cycle within an estuary, produce larvae that survive and develop over a wide range of salinities with negligible short-term (18 h) salinity-related mortality (Longley 1994). Spotted seatrout larvae tolerate brackish water or salinities lower than seawater better than hypersaline conditions (Killam et al. 1992). Juvenile red drum seem to tolerate brackish conditions better than adults, which are usually found offshore (Yokel 1966, Crocker et al. 1983). The ability to tolerate salinities lower than seawater has an obvious benefit in estuarine habitats. Here, rapid salinity fluctuations and brackish conditions due to storms and flooding are more likely than hypersaline conditions due to drought and evaporation (Killam et al. 1992). The high regulatory capacity of larval red drum and other larvae may be important in permitting their dispersal through estuarine waters and in allowing them to accommodate to the variable salinity of surface waters where much of their planktonic existence is spent (Holliday 1971, Longley 1994). When larvae metamorphose, there is an increased ability to survive in low salinities, although survival in high salinities is reduced. Changes in the structure of the skin of larvae renders it unsuitable for either ionic or gaseous exchange. These exchange functions become confined to the gills in older larvae and juveniles, and therefore, the surface area available for ionic transfer is reduced.

Salinity can affect the amount of energy required for body maintenance by increasing the metabolic cost of regulating internal body salts (Lankford and Targett 1994, Longley 1994). During periods of salinity stress, an increase in energy requirements may affect metabolism, activity, and the endocrine system of some estuarine organisms which may, in turn, influence their foraging activity, assimilation, growth, reproduction, and general well-being (Holliday 1972, Wohlschlag and Wakeman 1978, Wakeman and Wohlschlag 1983, Longley 1994). The respiration rates of adult blue crabs are significantly higher at 10‰ and 20‰ than at 30‰, which corresponds to the greater energy demands of osmotic regulation at lower salinities (Findley et al. 1978). Experiments with adult spotted seatrout, sand seatrout *Cynoscion arenarius*, red drum, black drum *Pogonias cromis*, sheepshead *Archosargus probatocephalus*, and Atlantic croaker show that metabolic activity can be reduced to critical levels when salinity deviates from optimum levels of 20-30‰ (Longley 1994).

Adaptation.

Geographically separate populations of a species may exhibit differences in salinity tolerance due to adaptation (Chanley 1958, Vernberg 1981). Adaptations are alterations in structure or function resulting from natural selection that confer survival superiority to the populations in which they occur (Smith 1960, McFarland et al. 1979).

Adaptations may allow some populations to survive salinity conditions which would severely stress or even kill other populations of the same species. American oysters from South Bay, Texas, for example, are able to live successfully at salinities >40‰ (Gray et al. 1991b), whereas most oysters exposed to these salinities would die or discontinue feeding and reproduction (Stanley and Sellers 1986). Genetic differences in the ability to tolerate salinity have been found in American oyster larvae between populations from low salinity and intermediate-salinity environments (Newkirk et al. 1977). Salinity requirements and preferences of pink shrimp, bay anchovy *Anchoa mitchilli*, inland silversides, Atlantic croaker, red drum, and sheepshead minnow *Cyprinodon variegatus* also appear to vary with geographic area (Costello and Allen 1970, Crocker et al. 1981, Pattillo et al. 1994).

Adaptive behavior may also be important in salinity selection by some estuarine organisms (Prosser 1973). Postlarvae of the pink shrimp, which hatch in the sea and enter estuaries as larvae, tend to swim toward shore and low salinity and can perceive salinities differences as little as 1‰ between water masses (Hughes 1969). They also showed an "aversion" to moving into a water mass of lower salinity. Juveniles and subadults, as they later return to the sea, swim against tidal currents in high salinities, but when salinities are low, swimming is with the current and gives way to passive drifting. Vertical migration in response to salinity gradients in offshore waters has been noted in larval spot and may be a mechanism to regulate their depth in the water column in order to maximize their presence in onshore-flowing waters, thus minimizing transport time into estuarine nursery areas (De Vries et al. 1995).

Effects of Salinity on Distribution

The observation of changes in area populations due strictly to salinity is complicated by organisms whose abundance and distribution vary with seasons and successes of recruitment, short life cycles, and wide-ranging pelagic larvae (Andrews 1973). However, numerous studies have demonstrated a correlation between the salinity tolerance limits of benthic and pelagic organisms and their distribution in an estuary (Vernberg 1981). The intermediate and fluctuating salinities typical of estuaries keep the number of species low because they prevent stenohaline marine and freshwater species from penetrating very far into estuarine systems (Moyle and Cech 1982, Deaton and Greenberg 1986). As a consequence, brackish areas of estuaries are poor in species, containing fewer numbers than marine waters and much fewer than freshwater (Remane and Schlieper 1971).

Direct Effects.

The paucity of species in estuaries is caused by variable salinities which create a physiological barrier to many organisms, and thereby, directly influence their distribution (Pearse and Gunter 1957, Andrews 1973, Levinton 1982, Moyle and Cech 1982). As a result, a large number of organisms are distributed in fairly definite zones or assemblages that reflect their responses and adaptations to the salinity gradients present in estuaries. Salinity gradients in estuaries undergo long-term variation due to severe droughts, floods, chronic inflow reductions, brine discharge, channelization, etc. and can have a dominating effect on distribution (Andrews 1973, Czapla et al. 1991, Longley 1994). The effects of salinity changes are particularly pronounced on those species that spend their entire lives in an estuary (e.g., stone crabs *Menippe* sp., grass shrimp *Palaemonetes* sp., spotted seatrout, gobies *Gobiosoma* sp.), on young animals with limited mobility that utilize the estuary as a nursery area (e.g., larvae of penaeid shrimp, gulf menhaden, pinfish, Atlantic croaker), and on relatively stationary benthic fauna (e.g., American oyster, common rangia, hard clams). High salinity on the lower

Texas coast is believed to limit the population of American oysters in the Laguna Madre, where freshwater inflow is low and salinities of >45‰ are common (Longley 1994). On the other hand, exposure to low salinity (<2‰) for an extended period of time causes high oyster mortality (Stanley and Sellers 1986). Dredging can cause long-term changes in salinity by allowing the intrusion of saltwater into brackish water habitats. Such intrusions can cause population declines of the common rangia, which thrive in low salinity habitats (Harrel 1993). Juvenile brown shrimp appear to prefer the more saline regions of an estuary (24.2 to 26.2‰), and will move to deeper, high salinity waters when salinity levels in salt marshes drop due to increases in freshwater inflow (Longley 1994). White shrimp juveniles tend to be more common in the middle to upper reaches of the estuary where salinities are generally low (<10‰) (Williams 1955, Gunter et al. 1964, Longley 1994).

Indirect Effects.

Salinity can also influence animal distributions indirectly through its effects on habitat. Habitat plays an important role in determining the distribution of plants and animals, and habitat alteration can have profound effects on those species present (Smith 1980, Ross and Epperly 1985, Gray et al. 1991b, Quammen and Onuf 1993, Longley 1994). Although estuarine residents may tolerate changes in an estuary's salinity pattern, they may not be able to withstand such changes if their habitat is destroyed or displaced. Loss or modification of critical habitat can result in increased mortality from predation, lower adult recruitment levels, and a decline in species numbers. Two such habitats that are subject to modification due to changes in salinity are submerged aquatic vegetation (seagrass beds) and emergent vegetation (salt marshes). Both habitats are important to many estuarine organisms (e.g. penaeid shrimp, juvenile blue crabs, pipefish *Syngnathus* sp., gobies, pinfish, gray snapper *Lutjanus griseus*, red drum, and spotted seatrout, etc.) as sources of food, refuges from predation, and as spawning sites (Simmons 1957, Odum 1971, Zieman 1982, Sheridan and Livingston 1983, Gosselink 1984, Huh and Kitting 1985, Zimmerman et al. 1990, Pezeshki and DeLaune 1991, Quammen and Onuf 1993, Longley 1994). Plants associated with estuarine habitats have specific salinity requirements, and changes in the salinity regime of an estuary can cause declines in their abundance (Kutkuhn 1966, Deegan et al. 1986, Quammen and Onuf 1993, Longley 1994). Changes in the salinity regime could influence the abundance of animals dependent on affected habitats when the total area of habitat in an estuary declines (Kutkuhn 1966, Dugan 1983, Ross and Epperly 1985, Knox 1986, Quammen and Onuf 1993, Adair et al. 1994, Longley 1994, McIvor et al. 1994). In Florida Bay, reductions of benthic vegetation due to salinity fluctuations are associated with declines of estuarine fauna (Montague and Ley 1993, McIvor et al. 1994).

Oyster beds and reefs provide other important habitats in estuaries (Wells 1961, Smith 1980, Zimmerman et al. 1989). These areas are also heavily utilized as food sources and refuges from predation for such species as stone crabs, spotted seatrout, gobies, and gulf toadfish *Opsanus beta* (Wells 1961, Hoese and Moore 1977, Van Hoose 1987, Bert and Harrison 1988, McMichael and Peters 1989, Zimmerman et al. 1989, Longley 1994). The distribution of oysters is profoundly influenced by salinity patterns which change either from natural or anthropogenic events (Gunter 1953, Wells 1961, Andrews 1973, Chatry and Millard 1986, Mueller and Matthews 1987, Gray et al. 1991b). Both high- and low-salinity events can have serious repercussions on the distribution of organisms that inhabit the oyster reef habitat. When salinity increases for long periods of time, high oyster mortality can result from increased numbers of stenohaline predators and parasites invading the reef. In response to higher salinities, the highest concentration of oyster reefs may shift over time to upper bay areas (Mueller and Matthews 1987). In the upper estuary, oysters and the organisms living on oyster reefs are much more susceptible to freshwater kills, runoff pollution, and siltation due to their proximity to sources of freshwater input. Periodic freshets are needed to control detrimental organisms invading the reef and to keep it healthy (Cake 1983, Chatry and Millard 1986). However, decreases in estuarine salinity for long periods (i.e., weeks) can cause oysters to perish from osmotic stress or starvation.

Populations Outside their Range of Tolerance.

Many estuaries are subject to strong tidal influence which cause wide daily fluctuations in salinity. Despite this, some species can live in such areas, which have average salinities that would normally be fatal. Organisms are able to survive in areas with salinity levels outside their limits of tolerance, if periods of temporarily tolerable salinity are sufficient for feeding, defecation, and reproduction (Kinne 1971). The American oyster and the hard clam are able to shut their shells and respire anaerobically during periods of salinity extremes. When salinities moderate, they can reopen and begin filter feeding again. Changes in the tidal patterns of an estuary could cause populations living on the edge of their tolerance range to decline or perish.

<u>Food Resources/Prey Distribution</u>

Ecological as well as strictly physiological factors can influence an organism's response to estuarine salinity (Hildebrand 1957, Wells 1961, Hill 1976). A species capable of withstanding the prevailing salinity may be hindered from exploiting an area if the animals it preys upon are excluded due to osmotic stress. Benthic epifauna and infaunal animals (common rangia, hard clams, American oyster, annelid worms, and peracarid crustaceans, e.g. amphipods and tanaids) which are relatively sessile, can be wiped out in an area if high freshwater inflow causes an extended period (days) of low salinity. Where this has occurred, concurrent declines of small predators (shrimps, crabs, and small fishes) which feed on infauna have also been noted despite the abilities of these predators to osmoregulate (Zimmerman et al. 1990). Infauna predator species (e.g. penaeid shrimp, bay anchovy, gulf menhaden, gulf killifish, naked goby *Gobiosoma bosci*, striped mullet, and silversides *Menidia* sp.) are important forage items for large, economically important estuarine species such as blue crab, red drum, black drum, spotted seatrout, southern flounder *Paralichthys lethostigma*, etc. (Gunter 1945, Hildebrand 1943, Moore 1974, Benson 1982, LaSalle and de la Cruz 1985, Burrell 1986, Perschbacher and Strawn 1986, Eversole 1987 Longley 1994, Zimmerman et al. 1990, McTigue and Zimmerman 1991). Large, obligate carnivores rely on the presence of these small predators to meet their dietary needs, and the absence of suitable prey in a given region can result in predators moving out of the area in search of better feeding grounds (Longley 1994).

Salinity may also result in differential predation and cause varying numbers of prey among estuarine habitats (Weinstein and Walters 1981, Currin et al. 1984). Studies on the Atlantic coast have noted that highest mortality rates of small juvenile spot occur in high-salinity areas which coincide with maximum densities of predators on this species (silversides *Menidia* sp. and killifish *Fundulus* sp.). The American oyster also suffers greater predation in high salinity (>10-15‰) waters from stenohaline organisms such as starfish, oyster drills *Thais haemastoma*, lightning whelks *Busycon perversum*, and stone crabs *Menippe* sp. (Mueller and Matthews 1987, Longley 1994).

<u>Temperature effects</u>

When trying to determine the effects of salinity on animal distribution one must consider that an organism's tolerance to salinity changes in a laboratory setting can be much greater than that displayed in the natural environment (Vernberg and Coull 1981). For example, laboratory studies have shown the common rangia can withstand salinities up to 30‰, but they are rarely found over 18‰ under natural conditions (Parker 1966, Godcharles and Jaap 1973). For this reason, various combinations of environmental factors should be considered in order to determine the tolerance limits for salinities which more nearly approximate what an animal experiences in its natural habitat. Generally, the interaction of one or more factors will kill an organism at intensity levels that would be non-lethal if tested separately.

One such important factor is temperature. Temperature influences many of the processes involved in an animal's tolerance of salinity (Hill 1976). As a result, the range of salinity tolerance of some species varies with temperature, and at certain temperatures an animal's osmoregulatory abilities may completely breakdown. Several species are affected in this manner. For example, the tolerance of the American oyster to low salinity generally diminishes as water temperatures increase (Berrigan et al. 1991). At temperatures below 5° C, the American oyster is tolerant of low salinity, but will die after a few days in low-salinity waters when the temperature is 15° C.

Temperature extremes can significantly affect the ability of juvenile blue crabs and penaeid shrimp to tolerate salinities outside their preferred range (Turner and Brody 1983, Mulholland 1984, Longley 1994). Even at temperatures below 20° C, the salinity tolerance of brown shrimp is significantly narrowed (Copeland and Bechtel 1974).

The salinity tolerance of fishes also may be affected by temperature. Juvenile gulf menhaden appear to be influenced by salinity-temperature combinations (Copeland and Bechtel 1974). At high temperatures (>25° C), menhaden are abundant over a wider range of salinities than they are at lower temperatures, although at low salinities (<10‰) they are abundant over a wider range of temperatures than they are at higher salinities.

The inland silverside, which normally prefers low to medium salinities, usually occurs in high salinity areas of estuaries only during cool temperatures (Weinstein 1986).

Reproduction

Reproduction is a major physiological phenomenon that dominates all other processes for many species (Vernberg 1983). Although reproduction is not necessary to the survival of an individual, the continuance of a species depends upon its ability to reproduce. Therefore, although organisms may tolerate the salinity range of a particular habitat, they will be unable to establish a continuous presence unless they have the ability to propagate at prevailing salinities.

Many mobile species (e.g., striped mullet, spot, Atlantic croaker, sand seatrout, pinfish, sheepshead, flatfishes) avoid salinities unfavorable for reproduction by spawning in coastal or oceanic waters (Gunter 1945, Springer and Woodburn 1960, Gilbert 1986, Sogard et al. 1987, Sutter and McIlwain 1987). As can be seen in Table 1, the eggs and larvae of these species generally have a narrow range of salinity tolerance especially when compared to those species that spawn within the estuary. Oceanic and nearshore environments have a more stable salinity structure than estuaries and spawning in these areas gives eggs an opportunity to develop and larvae time to acquire osmoregulatory abilities to cope with more rapid changes in salinity (Vernberg and Vernberg 1981, Longley 1994).

Salinity may affect reproduction during any one of three stages: gamete development, eggs through hatching, and larvae after release into the aquatic environment (Longley 1994). These stages are generally more vulnerable to fluctuations in salinity because they have narrower ranges of salinity tolerance than juvenile and adult stages (Table 1).

Gamete Development.

Reproductive failure in oysters can be a direct result of salinity inhibiting gamete development, or caused indirectly by insufficient feeding at low salinity (Sellers and Stanley 1984). Gametogenesis in this species does not occur if the salinity is less than 6‰ (Butler 1949), and the optimum for survival and reproduction is approximately 15‰ (Chanley 1958, Galtsoff 1964). Spawning in the common rangia will not occur unless a rapid salinity change occurs, either a sharp increase or decrease in ambient salinity (Cain 1975). Salinity appears to affect both the maturation and spawning age of daggerblade grass shrimp *Palaemonetes pugio* (Alon and Stancyk 1982); individuals from high-salinity waters reach maturity faster than those in low-salinity waters. Striped mullet is evidently unable to reproduce successfully at low salinities (Christmas and Waller 1973). Early ovarian development and endocrine function in female spotted seatrout are significantly altered by salinities outside their optimum range (Thomas and Boyd 1989).

Eggs Through Spawning.

After spawning, the embryonic development of eggs can also be negatively affected by salinity (Thomas and Boyd 1989, Longley 1994). Eggs of the hard clam will only develop into straight-hinged veligers within a salinity range of 26.5 to 27.5‰ (Mulholland 1984). Egg development in the bay scallop is successful at 25‰, but no embryonic development occurs at 10‰ or 15‰ (Castagna 1975, Tettlebach and Rhodes 1981). In May 1991, no ovigerous gulf stone crab *Menippe adinia* females were observed in Mississippi Sound when salinities dropped to 10‰ (Brown and Bert 1993). The low salinity during this period may have had a negative impact on gravid or ovigerous females, the embryos, or the larvae causing this absence. The blue crab can live in or near water that is essentially fresh, but must return to the ocean to spawn because the eggs cannot develop in fresh water (Sandoz and Rogers 1944). Blue crab eggs in salinities above or below the optimum range of 23-30‰ either do not hatch or produce premature larvae that die in a prezoeal stage (Sandoz and Rogers 1944, Van Engel 1958). Embryos and early larvae of the common rangia have poor survival unless the salinity is between 2 and 10‰ (Cain 1975). The spawning success of both spotted seatrout and red drum are adversely affected by extreme salinities, which can occur in estuaries during drought conditions or periods of high freshwater inflow (Simmons 1957, Shepard 1986, Thomas and Boyd 1989, Gray et al. 1991a, pers. comm. Robert Vega, GCCA/CPL Mar. Develop. Ctr., Corpus Christi, TX 78418). Salinity extremes can also impair the buoyancy of the pelagic eggs of red drum and spotted seatrout thus affecting their movement into bay and estuary nursery areas by currents, tides, and other physical factors (Perret, et al. 1980, Holt et al. 1981, Vetter et al. 1983, Gray and Colura 1988, Longley 1994). Females of ovoviviparous species, such as the bull shark *Carcharhinus leucas* and fishes in the family Poecilidae, are able to protect their developing eggs from variable salinity by incubating them inside their bodies (Hoese and Moore 1977).

Larvae.

Salinity fluctuations often affect larval forms more severely than adults (Smith 1980). For example, grass shrimp, which can survive over a broad range of salinities as juveniles or adults, have poor survival rates as larvae in salinities less than 15‰ (Kirby and Knowlton 1976, McKenney and Neff 1979). The timing and intensity of spat setting for American oyster are also affected by salinity (Hopkins 1931, Chatry et al. 1983). Larvae of the inland silverside do not survive past the yolk sac stage at 17‰, but show no adverse effects at about 8‰ (Weinstein 1986). The more developed megalopae of the blue crab are able to withstand greater salinity extremes (_4‰) than earlier zoeae stages (_20 ‰) (Perry 1975). Larvae of gulf killifish, spotted seatrout, and Atlantic croaker hatch out over a wide salinity range, but abnormalities increase and survival declines as salinity deviates from optimum levels (Holt et al. 1981, Thomas and Boyd 1989, Perschbacher et al. 1990). Periods of high rainfall and low salinity in Florida estuaries lead to increased growth and survival of spotted seatrout larvae and juveniles and improved recruitment, whereas recruitment declines when rainfall is low and hypersaline conditions exist (Rutherford et al. 1989). Eggs or early larvae spawned by organisms in an oceanic environment and entering an estuary can be detrimentally affected by major changes in salinity caused by alterations in freshwater inflow (Longley 1994). Many estuarine dependent organisms require areas of low salinity for nursery grounds. Increases in the salinity of estuarine nursery areas may result in poor larval survival, leading to reductions in recruitment and population shifts. The distribution and abundance of the blue crab and penaeid shrimp are dependent on the presence of low salinity estuarine areas (Pearse and Gunter 1957). Increased salinities adversely affect white shrimp nursery grounds and can cause a shift in species dominance from white shrimp to brown shrimp, whereas periods of high river inflow coincide with high white shrimp production years (Longley 1994). The reduction of freshwater inflow and its nutrients could cause a decline in blue crab numbers due to fewer numbers of eggs hatching and reduced larval survival (Oesterling and Evink 1977).

The duration of larval development can be affected by salinity, and the effects can vary greatly among species. Larval development may be either accelerated or retarded by salinity (Holliday 1971, Sastry 1983, Longley 1994). For example, as salinity is lowered below an optimum of 20 to 22‰, maturation rates of American oyster larvae decrease progressively, which increases mortality and the period from hatching to settling (Hopkins 1931, Davis 1958, Longley 1994). In the laboratory, development to the first crab stage by grapsid crab larvae took several days longer when salinities were extreme (<10‰ or >40‰) (Schuh and Diesel 1995). First and median hatching times for gulf killifish take several days longer at high salinities (60-80‰) than at levels below 35‰ (Perschbacher et al. 1990). In addition to effects caused by extreme salinities, synergistic interactions of multiple environmental factors (temperature, dissolved oxygen, etc.) can affect larval development at salinity levels that are otherwise tolerated (Sastry 1983).

The survival of the eggs and larvae of some species may be influenced by maternal acclimation salinities as well as differences in osmoregulatory abilities of separate populations of a species (Holt et al. 1981, Vernberg 1983, Holt and Banks 1989, Longley 1994). When American oyster larvae spawned in different salinities were transferred to low-salinity water, those larvae originally spawned in low salinity had the highest survival rate. Eggs produced by a pair of spotted seatrout accustomed to salinities ranging from 10 to 25‰ showed the greatest rate of survival in nearly the same salinity range (Gray and Colura 1988). Red drum eggs spawned in a laboratory showed the best hatch-out rate at salinities near those of the maturation and spawning tanks of the parents (Holt et al. 1981). Differences in salinity tolerance displayed by populations of sheepshead minnow may result from separate groups being exposed to the different levels of environmental factors during their life cycle (Martin 1968).

Growth

Although not well studied, the effects of salinity on growth have been documented for a few estuarine species. The growth rate of several species of estuarine organisms used in experimental studies (e.g. polychaetes, amphipods, carp, bream, etc.) has been noted to decrease suddenly at salinities other than 5 to 8‰ (Khlebovich 1969). Hard clams show optimum growth in salinities between 22 and 33‰, and little or no growth in salinities below 22‰ (Chanley 1958, Davis 1958, Craig et al. 1988). Postlarval and juvenile white shrimp display less growth and decreased survival at salinities greater than 35‰ (Zein-Eldin and Griffith 1969). The daggerblade grass shrimp has the least amount of growth in salinities between 22‰ and 28‰ and temperatures 15° C and lower (Wood 1967). Blue crab growth rates are significantly less at low salinities (_3‰) than at 15 and 30‰ (Tagatz 1968, Cadman and Weinstein 1988). Paradoxically, blue crabs in low salinity areas are usually larger than those from higher salinities (Steele 1979). Their larger size in low-salinity habitats may be due to a greater intake of freshwater during each molt, which serves to expand the new shell, working in conjunction with the higher temperatures of the shallow waters found in these areas. The intermolt periods of megalopae decrease with salinity, which results in a shorter megalopal stage in low-salinity areas (Forward et al. 1994). Recruitment of spotted seatrout is thought to improve during high rainfall because growth and survival of larvae and juveniles increase in low salinities (Rutherford et al. 1989). Fluctuations of salinity in the range of 10 to 30‰ often promote more rapid growth of American oysters than a relatively constant salinity (Longley 1994).

CONCLUSIONS

Salinity affects every major aspect of the lives of estuarine organisms and is a key factor in determining suitable estuarine habitat. However, information on the salinity requirements of many estuarine species is not well known. The need for this information is becoming increasingly important as man-made modifications (e.g. channelization, dams, and flow diversions) continually change the salinity structure of many of the estuarine systems of the U.S.A. In order to effectively plan and manage for these modifications to reduce detrimental effects to the estuarine fauna, additional data are needed about the effects of salinity on estuarine animals and how animals respond to salinity changes.

To help provide for this need, information was summarized on the salinity requirements of 56 species (5 molluscs, 9 crustaceans, 42 fishes) that utilize estuaries (Table 1). Although many other species met the criteria for inclusion in the table, they were omitted due to a lack of information. A few species were included in the table despite having only limited information to illustrate how little data are available for some estuarine species. In general, little or no salinity data were available for species with no direct economic value, even though these species are ecologically important.

Our review of this topic has led us to draw the following conclusions:

1) Fluctuations in salinity are an integral part of the estuarine environment, and estuarine organisms have evolved a characteristic set of mechanisms for responding to these variations. Responses to salinity by estuarine animals occur throughout their life cycle on both a physiological and behavioral level by means of several different processes. The capacity of each of these processes and their interaction with one another determines the ability of an organism to tolerate the effects of salinity.

2) Salinity tolerance is also influenced by acclimation, adaptation, stage of development, environmental conditions, and the rate and magnitude of salinity change. Different populations of a species appear to have adapted to the specific salinity regime of their area and their tolerance to salinity may differ from that of other populations. As a result, the Gulf-wide salinity ranges in Table 1 may not accurately describe the tolerance of specific populations.

3) Although it is an important aspect in determining the effects of salinity on a species, the life stages of estuarine organisms are not well known. As seen in Table 1, much of

the well-supported data, even among better-studied species, is limited to the juvenile and adult life stages, whereas information concerning the salinity requirements of spawning, egg hatching, and larvae/pre-juvenile stages is either lacking, limited, or inferred based on other life history information. Based on the limited data now available, it appears that the eggs and larvae of those species that spawn in coastal or offshore waters tend to have relatively narrow ranges of salinity tolerance, whereas species that spawn in estuaries produce eggs and larvae capable of tolerating much broader ranges of salinity.

4) Organisms that complete their life cycle within estuaries are usually euryhaline throughout their development. However, salinity tolerance doesn't peak until actual estuarine residence begins in organisms that utilize the estuary for only a portion of their life cycle .

5) The salinity tolerance of estuarine animals generally becomes greater as they develop into adults. The ranges recorded in Table 1 indicate that egg and larval stages of most of the species surveyed do not survive over as wide a range of salinity as juvenile and adult stages. This tends to make egg and larval stages more vulnerable to salinity fluctuation. Data in Table 1 also shows that, in the majority of cases, most of an organism's tolerance ability has developed by the juvenile stage.

6) Estuarine animals exist together in a community assemblage, thus the influence of salinity on one species can be extended either directly or indirectly to affect other species. Salinity dictates the distribution of life in estuaries because of its intimate interaction with both individual and groups of species.

Salinity has a pervasive influence on the lives of estuarine organisms. Therefore, a thorough understanding of its effects on the biota is necessary to effectively manage both the physical and biotic resources of this nation's estuaries. Further research is needed on many estuarine species where data are incomplete or lacking, particularly those species considered to have little direct economic value. Many of these species have ecological importance, and their well being may indirectly affect the health of economically important species. Research should be focused on the early life stages (eggs, larvae) of organisms about which information is lacking for many species.

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	Life Stage	Spawning				Egg Hatching				Larvae/Pre-juvenile				
SPECIES		Range	Source(s)	Optimum	Source(s)	Range	Source(s)	Optimum	Source(s)	Range	Source(s)	Optimum	Source(s)	Range
Molluscs														
Argopecten irradians	bay scallop					**22-35**	26,200			**22-35**	138,200	**25**	200	**10-35**
Crassostrea virginica	American oyster	**2-40**	20,51	**12-30**	62,116,138	**7.5-34**	27	**10-22**	27	**5-39**	27,28	**20-30**	27,28,95	**2-43.5**
Rangia cuneata	Atlantic rangia	**1-15**	135	**6-10***	24	**2-15***	24	**6-10**	24	**2-20**	24	**10-20**	24	**0-30**
Mercenaria sp.	hard clam	**20-36***	45,222,223	**26.5-27.5***	45	**20-33**	45	**26.5-27.5**	45	**15-35**	117	**17.5-35**	27,138	**12-35***
Lolliguncula brevis	bay squid	**20-36***	7			**20-36***	7			**20-36**	7,209	**26-32**	7,209	**17.5-36**
Crustaceans														
Penaeus aztecus	brown shrimp	**24.1-36***	34	**30-35***	138	**24.1-38***	34	**30-35***	138	**24.1-36**	34			**0-70**
Penaeus duorarum	pink shrimp	**27-35**	34			**27-35**	34			**27-35**	34			**<1-47**
Penaeus setiferus	white shrimp	**27-35**	34			**27-35**	34			**27-35**	34			**0.3-48**
Palaemonetes pugio	daggerblade grass	**15-35***	221			**2.3-33.9***	2,221			**3-33**	2,124	**17-25**	2,105,108,124	**0-55**
Palaemonetes vulgaris	marsh grass shrimp									**5-35**	2,107	**20**	2	
Palaemonetes intermediu	brackish grass shrimp									**10-30**	172	**20**	2	
Menippe adina	gulf stone crab	**14-34**	188			**14-34***	21,188			**9-30**	188	**15-30**	188	**10-40**
Callinectes sapidus	blue crab	**23-33**	169	**22-28***	169,207	**23-32.6**	169	**22-28**	169,207	**5-40**	13,40,142	**20-31.1**	40,142,218	**0-60***
Callinectes similis	lesser blue crab	**25-37***	13,16			**25-37**	13,16			**11-37**	13,16	**24-37**	13	**0-37**
Fishes														
Dasyatis sabina	Atlantic stingray					**NA**		**NA**		**NA**		**NA**		**0-45**
Carcharhinus leucas	bull shark	**25-38***	32			**NA**		**NA**		**NA**		**NA**		**1.6-42***
Megalops atlanticus	tarpon	**28.5-39***	225			**28.5-39**	180,212,225			**28.5-39**	180,212,225			**0-47**
Myrophis punctatus	speckled worm eel	**27-42**	53,91,114	**30-35**	114	**27-42***	53,91,114			**0-39.5**	53,81			**0-37**
Brevoortia patronus	gulf menhaden	**25-37**	173			**6-36**	30,58,206	**25-36**	30	**6-37**	29,30,206	**15-36**	30,175	**0-67**
Dorosoma cepedianum	gizzard shad	**0-0.05**	71,114			**0-0.05**	71,114			**0-0.5**	114			**0-25**
Anchoa mitchilli	bay anchovy	**1-45**	9,47,91,100	**10-37**	91,100,114	**1-45***	47,91,100	**15-37***	31,91,114,144	**0-45**	47,100,144,216	**1-35**	100,216	**0-80**
Harengula jaguana	scaled sardine	**25-40***	71,91,143			**25-40***	71,91,143			**25-40***	71,91,143			**1-40***
Arius felis	hardhead catfish	**13-30**	22,72,100			**1.8-37.2**	22,31,71	**>5**	31,147	**2-37.2**	22,31,71,141,215			**0-56**
Cyprinodon variegatus	sheepshead minno	**0.08-63.1**	119			**0-110**	119,161			**0-110**	119,161			**0-142.4**
Fundulus grandis	gulf killifish	**0-45**	31,177,199	**10-30**	211	**0-80**	98,147,199,211	**0-35**	147	**0-80**	147,199	**5-35**	147	**0-76.1**
Adinia xenica	diamond killifish	**0-37***	69											**0-48.2***
Lucania parva	rainwater killifish	**0-37***	103			**0-37***	103			**0-37***	103			**0-48.2**
Fundulus similis	longnose killifish	**0-37***	71,73,183			**0-37***	71,183			**0-37***	103,183			**0.3-76.1**
Fundulus pulvereus	bayou killifish	**0-37***	69											**0.4-47.6***
Fundulus jenkinsi	saltmarsh topminno													**0-20.6**
Membras martinica	rough silverside	**5-31.1**	63,114,120			**5-35***	63			**5-35***	63			**0-32.4**
Menidia beryllina	inland silverside	**0-31.5**	63,114,120	**0-0.5**	114	**0-35***	63,73			**0-31.5***	12,63,120,73	**2-8**	120	**0-35.6**
Centropomus undecimalis	snook	**>20-38***	1,110,174,204	**30-38***	110,174,204	**30-38**	110,174,204	**30-38***	110,174,204	**14.8-38**	110,174,202,20	**30-38***	110,174,204	**0-36**
Chaetodipterus faber	spadefish	**30-37***	99			**30-37***	99			**30-37***	99			**0-43.3**
Caranx hippos	crevalle jack	**30-38***	6,14			**30-38***	6,14			**30-38***	6,14			**0-60**
Trachinotus carolinus	Florida pompano	**30-38***	54			**31-37.7**	56			**31-37.7**	56			**1.3-50**
Orthopristis chrysoptera	pigfish	**25-35***	99			**25-35***	99			**25-35***	99			**0-44.1**
Lutjanus griseus	gray snapper	**30-38***	81,166			**32-36**	162,166			**0-35***	81,184,194	**30-38***	138,166	**0-66.6**
Archosargus probatoceph	sheepshead	**30-38***	160			**30-38***	160			**5-38***	31,160			**0-43.8**
Lagodon rhomboides	pinfish	**30-38***	44,168			**30-38***	44,168			**20-38***	44,168			**0.3-75**
Bairdiella chrysoura	silver perch	**14.3-35**	71,99,114			**14.3-37.4***	71,99,114			**<1-37.4**	99,104,114	**10-37.4**	99,104,114	**0-44.1**
Cynoscion arenarius	sand seatrout	**15-37***	42,94,146			**15-37**	42,94	**25-37***	42,94	**0-36**	134,189	**15-36**	42	**0-34.5**
Cynoscion nebulosus	spotted seatrout	**7-45**	92,114,171,201	**15-35**	171,201	**0-50**	176,201	**15-38**	68,176,197	**0-50**	92,201	**20-35**	197	**0-48**
Leiostomus xanthurus	spot	**25-35**	89,114			**30-35**	152			**6-36**	42,89,104	**30-35***	152	**0-36.2**
Micropogonias undulatus	Atlantic croaker	**25-35**	114,201	**25-35**	201	**25-36**	114,201	**25-35**	201	**0-45**	13,42,92	**15-21**	13,201	**0-36.7**
Pogonias cromis	black drum	**10-31**	64,171	**24-30**	171	**8.8-34**	64	**23-34**	64	**0-36**	41,148			**0-80**
Sciaenops ocellatus	red drum	**14-40**	84,93,114,210	**28-37**	210	**10-40**	93	**30-36.5**	93	**8-40**	149,208,210	**28-37**	43,210	**0-50**
Mugil cephalus	striped mullet	**28-36.5**	57,193	**30-32***	132,193	**28-36.5**	57,193	**30-35**	131,193	**16-36.5**	57,193,216	**26-33**	131,134,193	**0-75**
Mugil curema	white mullet	**30-37**	4,129			**30-37**	4			**30-38***	4,129			**0-49**
Gobiosoma robustum	code goby	**10-30**	46,47			**10-40***	46,47			**10-40***	46,47			**10-40***
Gobiosoma bosc	naked goby	**10-30**	46,47			**10-40***	46,47			**1.2-40***	46,47,192			**0-45**
Opsanus beta	gulf toadfish	**2-40***	114			**2-40***	114			**2-40***	114			**1.8-42.9**

Juvenile			Adults			
Source(s)	Optimum	Source(s)	Range	Source(s)	Optimum	Source(s)
126,200	**16-35**	10,50,80,170,20	**10-35**	126,200	**16-35**	10,50,80,170,200
28,37,77			**2-43.5**	28,37,77	**14-30**	23,27,28
67,96,136	**5-18**	135,136	**0-30**	67,96,136	**5-18**	135,136
3,28	**20-36**	222,223	**12.5-36**	3,222,223	**20-36**	156,205,222,223
86	**25-30**	111	**17.5-36**	86	**25-30**	111
33,83	**>10**	34,36	**0.5-45.3**	33,90	**24-38.9**	34
76,194	**18-36**	36,76	**<1-69**	39,177	**25-45**	177,194
13,88,101	**<10**	74	**0.1-45.3**	13,90,76	**27-40***	13,130,138
183	**2-36**	105,218,221	**0-55**	105	**2-36**	2,105,218,221
			1-51	2	**15-35**	218
			5-60	2,177	**10-20**	48
21,177,188	**15-34**	21,188	**11.6-38.8**	90,155,177,188		
177,185	**0-20**	145,185	**0-67**	70,177	♂ **<10** ♀ **23-33**	206,217
13			**0-37**	13	**24-37**	13
19,146,185	**15-35**	71,141,191	**0-45**	177,198	**15-35**	71,191
102,182			**1.6-42***	102,182		
106,213	**5.1-22.3**	138	**0-47**	18,106,163,181	**5.1-22.3**	138
6,31,192,194,195	**17-37***	195	**0-42.4**	38,195	**17-37***	195
118,143,151,177	**5-30**	109,118,143	**5-67**	30,71,177	**5-35**	29,109,112
71,161,191,214	**0-15**	71	**0.05-41.3**	71,161	**0-15**	71
71,103,161,177,183	**10-40**	71	**0-80**	71,103,161,177,183	**10-40**	71
31,71,141,191	**>25**	71,141,143,191	**1-40***	31,61,71,141,191	**>25**	71,141,143
31,38,141,215	**5-35**	38,71,141	**0-60**	31,61,141,177,192	**15-30**	31,61,141,191,19
71,75,161	**10-30**	71,103,191	**0-142.4**	35,71,75,161,177,1	**10-25**	71,103,177,179,1
31,71,75	**2-25**	31,60,71,103,1	**0-76.1**	31,71,75,177	**2-25**	31,60,71,103,179
81,103,191	**10-30***	103	**0-48.2**	81,103,191	**10-30**	103
15,60,71,103,165,179	**2-15**	71,79,191,198	**0-48.2**	71,81,161,179,198	**2-15**	71,79,161,191,19
31,177,179,198	**10-25**	71,141,191	**0.3-76.1**	31,177,179,198	**10-30**	31,104,179,191
73,179			**0.4-47.6**	73,179		
31,179			**0-20.6**	31,179		
63,120,141,158	**15-30**	63	**0-36.6**	71,198	**15-30**	31,60,141,214
63,78,103			**0-120**	177,190	**15-30**	15,60,71,141
22,59,78,183,195	**10-30***	65,121,173,183	**0-41.4**	65,78,164,174	**20-36**	65,121
49,78,165,196	**15-30***	31,71,141,214	**0.3-43.3**	99,165,198	**25-37***	13,71,214
71,78,139,141,159,164,165	**10-37***	71,141	**0-60**	14,99,177	**30-38***	71
11,56,71,78,127,141,177,18	**20-37**	55,71,141,191	**1.3-35.6**	99,127	**32-36**	99
79,164,183,196	**20-37**	15,191	**12-56**	164,172,177,195	**25-38***	71
164,166,183,194,195	**5-37***	17,195	**0-47.7***	82,184,215	**30-38***	17,167
52,71,87,164,196,215	**1-40***	113,177	**0.3-43.8**	139,141,164	**1-40***	113,177
25,71,79,164, 177,	**5-38***	215	**0-75**	25,71,79,164,177	**20-38***	215
128,164,215	**20-35.5**	71,104,183	**0-48**	99,104,128,164,195,21	**30-38***	104,128
31,215	**<20**	31	**0-45**	31,71,177	**12-35**	13
20,125,166,215	**8-25**	150	**0.2-75**	141,177	**20-25**	115,220
104,196,215	**5-36**	133,141,191	**0-60**	13,177,196	**15-30**	104,133,141,217
71,137,196,215,216	**10-20**	52,71,191	**0-75**	71,137,177,196	**15-20***	31,99
123,177	**9-26**	123,148	**0-80**	177,178	**9-26**	123
43,71,140,141,149,177	**15-35**	43,71,140,224	**0-50**	140,177,178,216	**20-40**	178,216
71,85,90,161,177,192	**5-25**	13,31,71,141	**0-75**	85,90,161,177	**26-35***	133,216
159,195,196			**0-45**	177,196	**25-35***	71
46,47			**2.1-37.6**	46,103,158,183,215	**22-32**	15,46,183
172,198	**15-25**	13,60	**0-45**	177,198	**0-10**	46,60
15,75,103,158,191	**20-30***	141,183	**1.8-38***	14,103,177,191	**20-30***	141,183

Achirus lineatus	lined sole	**25-37***	97,195			**25-37***	97,195			**25-37***	97,195			**1.8-43**
Symphuris plagiusa	blackcheek tonguef	**15-38***	120			**15-38***	120			**11-22**	120			**2.0-37.6**
Paralichthys albigutta	gulf flounder	**25-38***	66,203			**23-40***	66,153,203			**22-38***	203,219			**6-60**
Paralichthys lethostigma	southern flounder	**25-38***	51,87			**23-40***	5,153			**10-30**	5,186	**25-30**	186	**0-60**
*** best estimate based on life history information**														

49,71,103,164,183	**>15**	71,183	**2.5-43**	71,164,183	**>15**	71,183
15,103,120,157,183,190	**5-15**	183	**0-42.9**	31,60,71,165,194,195,19	**20-35**	71,78,79,177,192
71,154,158,179,183,196	**20-38***	71,177,183,215	**6-60**	13,71,158,177,183,187	**30-38***	13,71,177,183,21
13,31,177,187,192	**2-25**	31,71	**0-60**	31,81,177,192	**20-30**	138,216